

A DRAFT SYSTEM FOR THE IDENTIFICATION AND DESCRIPTION OF ARTHROPOD TRACKWAYS

by NIGEL H. TREWIN

ABSTRACT. The general morphological features of arthropod trackways are defined under headings of trackway width, imprint morphologies, track rows, repeat distance, symmetry, continuous marks, discontinuous marks and trackway curvature. These features are combined in a standard format for use in trackway description and diagnosis. The data can be used in a Trackway Data System, in which trackway attributes are represented by a formula of numbers and letters. The establishment of such a system and associated database would be a useful aid in identification and comparison of trackways using computer-based grouping or by construction of an Expert System. However, many genera will require redefinition and description before a sufficiently detailed database can be established.

ARTHROPOD trackways form a part of many trace-fossil assemblages, and pose particular problems for description and assignment to an ichnogenus. Many of the diagnoses in the literature are inadequate, in that they are either so general that they can accept a wide range of material, or else they contain such specific restrictions that the erected genus is likely to remain monospecific. Whilst the following analysis is applied to arthropod trackways, it could also be applied to the trackways of polychaete annelids.

There is no consensus on a preferred hierarchy of the elements composing a trackway, thus features such as size, imprint shapes, imprint series and continuous drag marks may be singled out, whilst other features are not included in description or diagnosis. A few publications deal almost exclusively with trackways. These include the privately published work of Smith (1909) and the revisions and descriptions of these Devonian traces by Walker (1985). Work on dominantly Permian traces by Walter (1983) introduced numerous new trackway names and a valiant attempt to order trackways into 'groups'. Hence he divided the *Cursichnia* (running tracks) of Müller (1962) into *Multipodichnia*, *Pentapodichnia*, *Tetrapodichnia* and *Tripodichnia*; placing greatest importance on the number of imprints occurring in groups or series in a trackway. Within these groups, Walter included or erected a number of genera and species. Müller (1962) extended the ethological classification of trace fossils by Seilacher (1953) to present a major group *Movichnia* (movement traces) which he subdivided into four sub-groups representing flying (*Volichnia*), swimming (*Natichnia*), running (*Cursichnia*) and crawling (*Repichnia*). In practice, it is frequently difficult to decide in which subgroup to place a trackway, and this classification is of more use for academic discussion than as a practical classification of traces. Similarly the complex classification scheme of Vyalov (1968) (summary in Häntzchel 1975) has not been adopted as a practical system. This contribution is not concerned with the question of classification, but with the problems associated with description and diagnosis of trackways in the broad sense.

It is generally at genus and species level that difficulties arise due to inadequate designations or restrictive designations based on one or two specimens. Such designations need to be constructed with sufficient latitude and clarity to provide a useful taxon, but not with such restrictions that make it unlikely that another trackway would ever be placed in that taxon.

The purpose of this contribution is to summarize the characteristics of trackways that should be included in descriptions and considered for diagnoses; and to provide a report form for use in trackway description, and in diagnosis construction. A machine-readable Trackway Data System

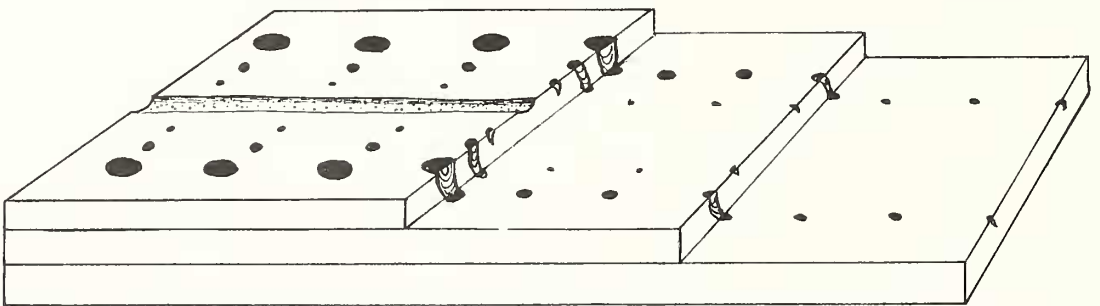
which reduces the main attributes of trackways to a simple formula is also introduced, and discussion is invited on the system before a working database is established.

TRACKWAY PRESERVATION

Prior to description of trackway components, it is necessary to consider the preservational aspects of the problem. Ichnotaxa are based on morphology and not on the originator; thus different preservational expressions of a track made by the same animal when walking on dry or wet sand, mud or silt, or in or out of water, will frequently fall in different taxa. Rolfe (1980) illustrated the marked differences in trackways of millipedes walking on wet mud and dry powder, and Sadler (1993) discussed differences in scorpion (*Hadrurus*) and spider (*Aphonopelma*) tracks on dry and damp sand. Experiments reported by Manton (1973, 1977) are most instructive in showing changes in gait and resulting trackways associated with speed of the animal, but trackways made on smoked glass cannot directly be compared with those on mud or sand. Appendages may be dragged in wet conditions but make discrete prints on a dry surface. In order for any impression to occur, the appendage must break the surface, and circumstances occur where only the heaviest foot-falls of the animal break the surface, the lighter ones leaving no impression. Temperature may even affect the activity and hence trackway of an arthropod, as observed by Brady (1947) in the case of the scorpion *Centruroides*. Thus, not every apparently well preserved trackway necessarily gives evidence of the number of legs used in locomotion.

Tracks commonly occur as epichnial impressions or can be moulded as convex hypichnia, and hence definitions of grooves or ridges must specify the preservation. It is recommended that trackways be described with respect to their epichnial preservational aspects. A trackway may change character markedly along its length, maybe due to change of substrate or a change in the activity of the animal. To avoid a plethora of names relating to the same track, it is proposed that the naming of the trackway should refer to the highest level of organization recognized, which is clearly repeated along the trackway. This practice has been followed effectively by authors with abundant material to study, thus Anderson discussed variation in *Petalichnus* (Anderson 1975) and *Umfolozia* (Anderson 1981) and avoided the creation of numerous supposedly new genera and species.

Trackways may also be preserved as undertracks and the more lightly impressed elements of the surface trackway may not be preserved in the undertrack (Text-fig. 1). Ideally, undertracks should



TEXT-FIG. 1. Diagram illustrating the variation of a hypothetical trackway in undertrack preservation due to different depths of impression of appendages.

not be given new generic names but be described as, for example, 'undertrack of *Paleohelcura*'. In practice it can be difficult to identify a specimen as an undertrack, and many have received names. Clearly, all morphologically distinct trackways should initially be named and described; later it might be shown that they are undertracks or some other preservational aspect of another trackway.

TRACKWAY COMPONENTS

The following breakdown of trackway components into eight sections follows, with additions, the work by Seilacher (1955) and Walter (1984). The terms used are illustrated in Text-figure 2. In trilobite work, a trackway may be referred to as a trail (e.g. Osgood 1970), but trail should be reserved for ribbon-like continuous traces lacking discrete leg imprints. Problems of definition do arise since trackways with defined prints can grade into ribbon-like traces as the maker moves from a damp to a wet substrate. Trilobites could plough through the surface sediment to leave *Cruziana* trails, or walk to give trackways. Clearly there is a gradation and definition becomes difficult, particularly since an arthropod may leave a continuous drag mark in addition to clear imprints. Such combinations are described here as trackways.

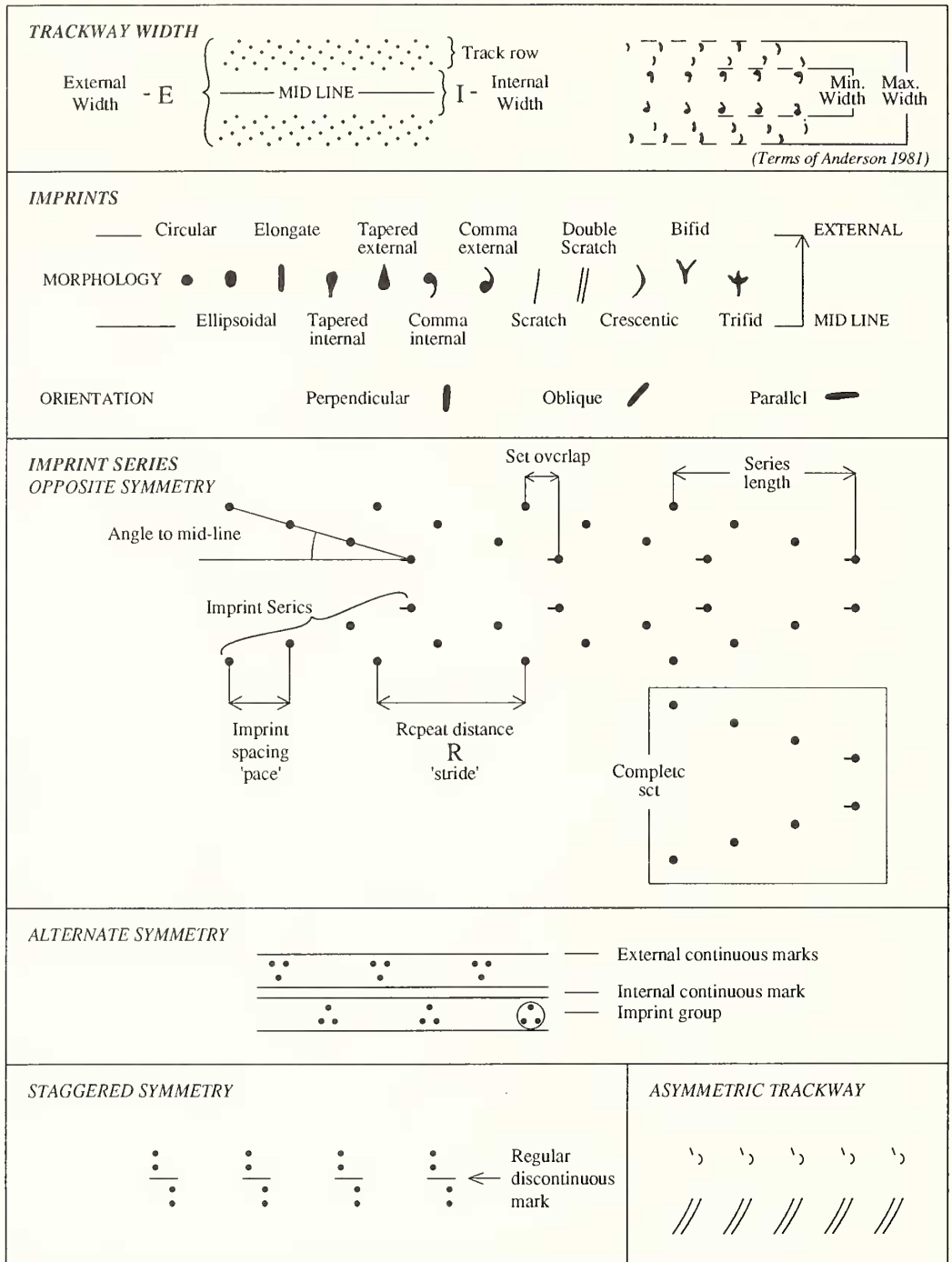
1. *Trackway width* (Text-fig. 2). In most trackways external and internal widths can be measured. In both cases it is useful to establish the range and mean of these values (e.g. Pollard 1985) and also to express them as a ratio. It is generally advantageous if absolute size is not used as an ichnogeneric discrimination, since this opens the way for unnecessary new genera, or may necessitate revision of diagnoses when identical material of a different size range is discovered. If the individual prints are elongate more detailed measurements can be made using the outer or inner extremities of prints within imprint series. In Anderson's (1981) study of *Umfolozia*, a minimum width at the outer extremity of the print pairs nearest the mid-lane was measured. Thus, internal width differs from minimum width (Text-fig. 2).

2. *Imprint morphologies* (Text-fig. 2). An imprint is the mark made by an element of a single appendage. This is frequently a locomotory appendage, but other parts of the animal may make regular imprints. Imprint morphology and orientation are frequently extremely variable within individual trackways. This can be the result of different character and action of appendages, or change in animal activity, or change in substrate. Where imprint shapes within a single trackway are highly and continuously variable in shape and orientation they have little potential for useful taxonomy. However, impressions of appendages bearing distinctive structures, such as bifid or trifid claws, provide useful diagnostic evidence. Osgood (1970) uses the terms proximal and distal (relative to the midline) in the description of imprint morphology. The presence of push-up mounds of sediment at the rear of leg imprints, or tic marks left by the drag of departing legs (Sadler 1993) may reveal the direction of motion, but caution must be exercised and it is frequently impossible to determine direction of motion. Thus the interpretation of direction of movement should not be part of the definition of the trackway.

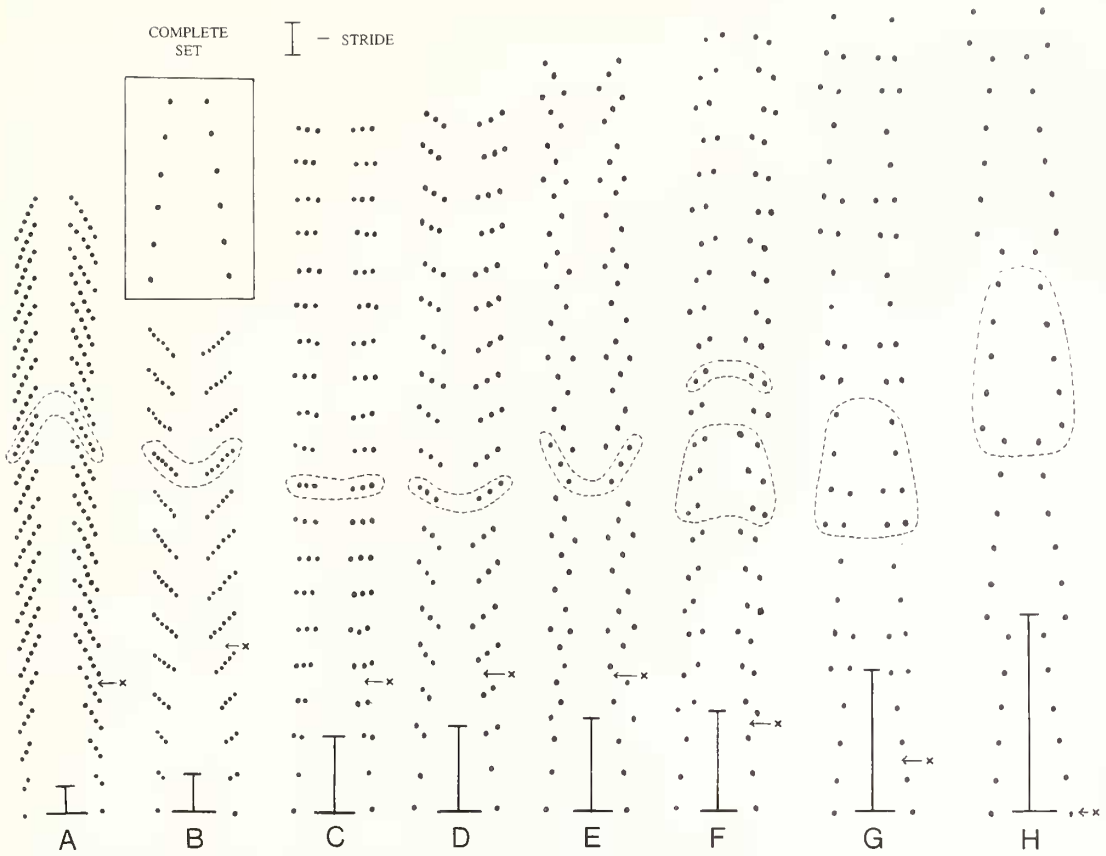
3. *Track Rows*. Recognition and interpretation of organization within track rows is important both for description and for interpretation of trackway originators. This was clearly recognized by Seilacher (1955) and Osgood (1970), and was used by Walter (1983) in his trackway classification.

Track rows can be regarded as simple (single row of imprints) or compound (several imprints in width of track row). The recognition of imprint series or groups (Text-fig. 2) raises the organizational status of a trackway, and such organization should be an important part of the diagnosis. In many trackways, organization can only be recognized or interpreted with confidence at trackway bends. False or apparent groups may result from coincidences in repeat length.

The concepts of Imprint Series and Imprint Groups can be confusing both from the requirements of description and interpretation. Series usually represent a movement phase of the animal using all appendages once, but groups do not necessarily represent the same situation. This feature is illustrated by Text-figure 3, which shows how trackway series can be wrongly described, resulting in a misinterpretation of the number of legs, morphology or gait of the arthropod. Text-figure 3 was constructed by taking a basic simple set of twelve prints, with series in straight lines at a low angle to the mid-line. Whilst this is a hypothetical set, it closely resembles those of *Petalichmus capensis* (nine to ten prints in a series, Anderson 1975) and *Umfolozia* (five prints in a series, Anderson 1981).



TEXT-FIG. 2. Diagram to illustrate the attributes of arthropod trackways and their terminology.



TEXT-FIG. 3. Hypothetical trackways produced by the repetition of a twelve-imprint set made of two oblique series of six. Repetition of the set upwards from the base of the figure using different repeat distances, or strides (the vertical lines) but with constant pace, produces a great variety of apparent, but false, series or groups, of which a few eye-catching examples are indicated enclosed in dotted lines. These false groupings mask the true nature of the complete set. The mark 'x' on each trackway represents the point at which the full pattern is developed by repetition of the set. Despite the somewhat artificial regular oblique nature of the imprint series of the set chosen, the results mimic closely effects seen in fossil trackways such as *Petalichmus* (in Anderson 1975) and *Umfolozia* (in Anderson 1981).

The trackways generated by variation of the Repeat Distance (the stride) are highly variable and produce false series or groups which can 'V' in either direction with respect to the mid-line and contain six, three or two prints (Text-fig. 3A-F). If both stride and pace are altered, further complexities arise. Only where there is little or no overlap between successive series does the true complete set become instantly recognizable (Text-fig. 3G-H). The experiments performed on living scorpions result in similar effects to those in Text-figure 3, as a result of differences in substrate, slope and activity of the animal (compare Sadler 1993, fig. 9).

The recognition of imprint groups is probably only valid for description in trackways which have an alternate or staggered symmetry. A pair of opposite imprint series was termed a complete set by Osgood (1970) and a trilsatz by Seilacher (1955). It is clearly important to recognize the form of the complete set if interpretations are made regarding leg numbers and direction of motion. Numbering of imprints within groups (e.g. Sadler 1993) may aid description, but imprint numbers will not generally relate to leg numbers on an arthropod, and are unlikely to be in a regular order

with respect to leg number. In the terminology of Anderson (1975) a series would be a natural track cycle.

Generally, there will be an appropriate taxon for a trackway lacking recognized organization in groups or series, but when the organization becomes recognized (e.g. at a bend) the trackway would be elevated to another taxon (e.g. Pollard 1985, p. 278 – *Diplichnites* to *Acripes*).

4. *Repeat distance*. For the full description of a trackway, it is important to identify the repeat distance of the trackway, representing the stride of the animal (Text-fig. 2). This is generally obtained from the repeat distance of a distinctive imprint or imprint pair in the track rows. In view of the variable width of trackways within a species or genus, it can also be usefully expressed in relation to trackway width. Variation may be found representing different gaits of the animal associated with different activities (walking, stalking, feeding or running). Both stride and the distance between successive imprints (pace) might also vary due to external conditions, such as substrate type, and the force and direction of the wind or water currents. Identification of repeat distance and interpretation of imprint series is essential for analysis of arthropod gait (e.g. Briggs *et al.* 1979). The term repeated track cycle of Anderson (1975) is not required if the set overlap (Text-fig. 2) is identified and related to the complete set.

5. *Symmetry*. Many trackways have a symmetry about the mid-line (Text-fig. 2) which can be described as opposite (where opposite legs move in phase as in a looper caterpillar, millipede, notostracan or trilobite), or alternate (where at least three legs are on the ground at any one time as in a spider, scorpion or insect) or an intermediate staggered arrangement. The staggered arrangement may arise due to a normal gait on a flat surface, but could also be due to trackway distortion caused by the animal walking across a slope, or battling against the wind or a water current.

Some trackways are characteristically asymmetrical (Text-fig. 2) due to the activity of the animal (e.g. sideways motion of a crab, or dissimilar function of limb rows). Such intrinsically asymmetrical trackways require separate description of the track rows or, if they lack two well defined track rows, may have to be described as a single complex track row and an outer and inner side defined.

6. *Continuous Marks*. Continuous marks can be defined as those which continue unbroken along the trackway length for several repeat distances (Text-fig. 2). In some trackways, they are so persistent as to be used as a prime element of the diagnosis (e.g. *Siskemia* in revision by Walker (1985)) whilst in others they are less prominent or irregularly broken or preserved. Frequently they will only be apparent in a surface track, the undertrack showing no continuous impressions. They may be useful in determining the morphology of the animal, and the way it moved and turned corners (e.g. the classic *Siskemia* turning tracks illustrated by Smith (1909) and Pollard and Walker (1984)).

For descriptive purposes continuous marks can be described with respect to their position relative to track rows (internal, external) and their mutual spacing. Internal continuous marks may be related to ploughing of the head or drag of a tail. Constant spacing may indicate a telson with rigid spines, and variable spacing the drag of a pair of independently moveable spines. External marks, more usually discontinuous, may be made by spines on the margin of the head (e.g. genal spines of trilobites) or by thoracic spines.

7. *Discontinuous Marks*. Discontinuous marks may display a regularity associated with the repeat distance of the trackway (e.g. *Petalichnus capensis* in Anderson 1975) and may be due to repeated dragging of an appendage. On a soft surface appendages may be dragged through the surface to leave such a mark, but on a firmer surface only a simple imprint might result. Irregular discontinuous marks may only appear rarely along the length of a trackway, but nevertheless provide information on the morphology of the trackway maker. Their use in taxonomy is restricted by their irregular nature.

8. *Trackway Curvature*. The overall directional nature of the trackway (Text-fig. 2) can provide useful material for description or diagnosis, and information on the morphology and behaviour of the animal. Trackway curvature, minimum turning circle, abrupt angular direction changes, mutually oriented trackways and meandering style are all features worthy of consideration.

ILLUSTRATION OF TRACKWAYS

Clearly there is requirement for good quality photographic illustration. Such illustration should also encompass the range of form of the ichnogenus or species being described and defined.

In view of the difficulty of lighting and photographing delicately impressed trackways on undulating surfaces, it is also suggested that photographs be augmented with drawings of both the actual trackway and the authors interpretation of the ideal form which corresponds with his diagnosis or description. This is frequently done, but seldom is any attempt made to illustrate range in variation, and the illustrated material of many species relies on a single specimen. The work of Anderson (1975, 1981) is an example of good practice, based on exceptionally well preserved material, and Sadler (1993) provides a well illustrated comparison between ancient and modern trackways.

DESCRIPTION REPORT FORM

The form (Text-fig. 4) presented here is an attempt to order trackway description. Whilst it is intended to maximize the information included in a description, it must be stressed that not all of the descriptive sections 1–8 on the form would need to be used in a diagnosis of an ichnogenus or species. The organization of the form is not intended to imply any hierarchy of features in terms of importance for generic or specific diagnoses. It is suggested below that numerical methods such as cluster analysis could be applied to the data, and hence an equal value is required for each variable.

DERIVATION OF A DESCRIPTIVE FORMULA

A further stage in the ordering of trackway descriptions and diagnoses is to produce machine-readable data which can be expressed as a simple formula. The descriptive framework of Text-figure 4 has been utilized to produce the Trackway Data System (Text-fig. 5), a checklist which enables all features to be reduced to a set of numbers and letters. Numbers represent the *Descriptive Sections* of Text-figure 4, and letters the *Attributes* (Text-fig. 2) within each section. The Attributes can be morphological (e.g. Text-fig. 5, Section 2.1) or contain chosen numerical ranges (e.g. Text-fig. 5, Sections 1, 3, 4). The ranges chosen have been based on a brief survey of described trackways in an attempt to produce ranges with practical application. The morphological characters (e.g. in Section 2.1) could certainly be expanded, but the addition of a category OTHER enables unusual characters to be written in. The number of possible variables on the form exceeds 120, and should be sufficient to describe and distinguish trackways.

Most formulae derived from this system will contain only a few of the Sections and Attributes present on the form and thus formulae are generally relatively simple. Text-figure 6 illustrates a few trackways and the formulae derived from them by use of the Trackway Data Sheet.

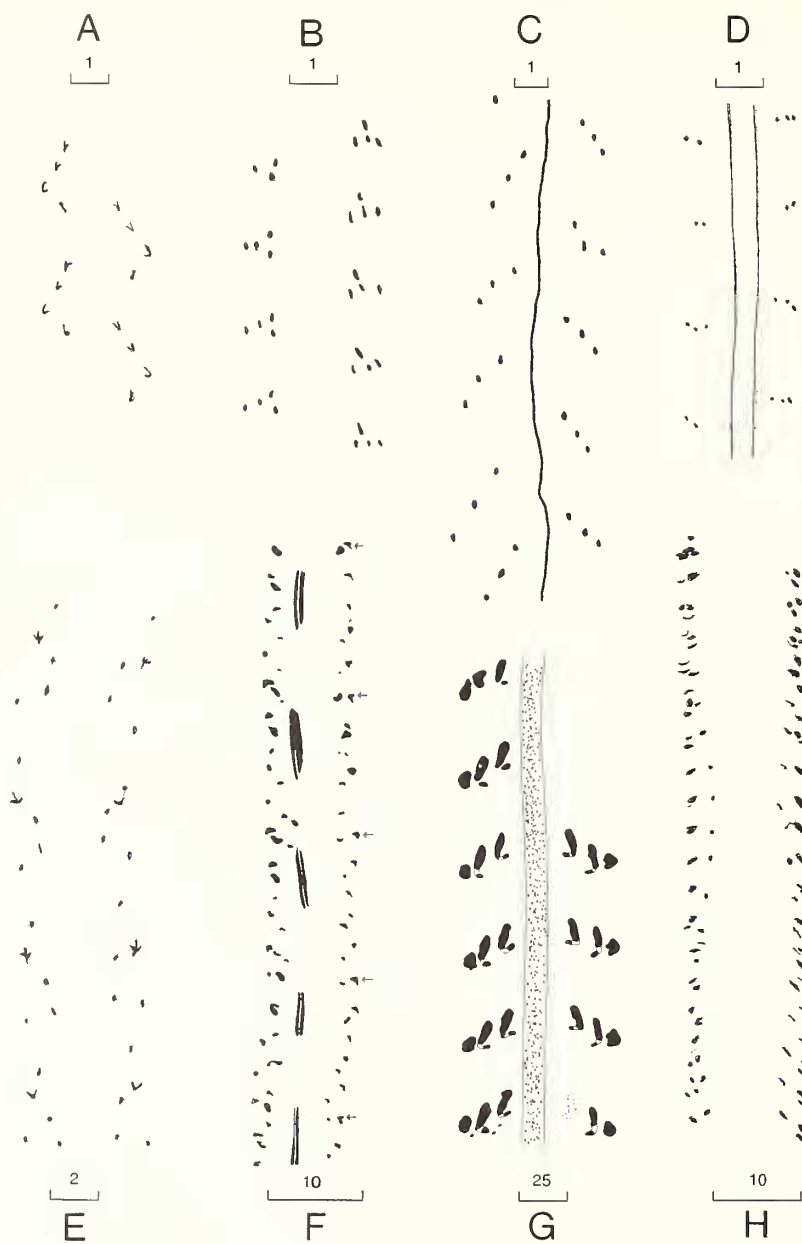
In using the Trackway Data System, it will often be found that a range in morphology of the trackway covers more than one Attribute, thus trackways with a width range of 20–80 mm would have the designation 1·1 B, C. Within the imprint morphology section, trackways will also frequently have imprints of more than one Attribute as illustrated on the Data Sheet.

In Section 3 of the form, simple track rows are those with only a single line of prints, which may or may not have recognizable series. Compound track rows have more than one imprint in the width of the track row; thus series overlap. In compound track rows, the number of imprints in a unit length of the trackway equal to its external width (E) can be counted. This is independent of size and can be counted in all compound trackways whether or not series or groups are described.

In Section 4, the Repeat Distance or stride is measured and related to the trackway width. Thus trackways with a repeat distance less than the trackway width (E) have values greater than unity

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TEXT-FIG. 5. Form for the reduction of arthropod trackway descriptions to a format suitable for computer storage and comparison (see text).



Trackway Components	1		2		3			4	5	6	7		8
	1.1	1.2	2.1	2.2	3.1	3.2	3.3				7.1	7.2	
<i>Trackways</i>													
A	B	C	BL	Y	-	-	CY	B	B	-	-	-	A
B	B	B	B	YZ	-	-	DY	D	B	-	-	-	A
C	C	D	A	V	-	-	CX	B	B	A	-	-	A
D	B	B	A	V	-	-	WX	BC	C	B	-	-	AB
E	C	B	BN	ZY	-	-	CL	A	A	-	-	-	AB
F	CD	B	BCFGY	XY	-	-	DN	A	A	-	A	-	AB
G	E	D	ACM	Y	-	-	DJ	D	A	A	-	-	A
H	D	B	ABCDF	XY	-	AE	-	-	A	-	-	-	AB

TEXT-FIG. 6. For legend see opposite.

(Text-fig. 6B), and those with a repeat distance greater than the trackway width have values less than unity (Text-fig. 6E).

The main advantage of using such a system is that it greatly facilitates data comparison. This system could be utilized for simple cluster analysis programmes to show dissimilarity, and hence attempt a computer-based grouping. More usefully, it could be used to construct an Expert System whereby identifications could be made by the interrogation of the data base. At the simplest level this would enable anybody to request possible names for: 'a 30 mm wide trackway with two parallel internal grooves, track rows with circular and elongate imprints in groups of three with alternate trackway symmetry and a repeat distance of 25 mm'. The answer to such an input would come back as *Siskemia* Smith, 1909. As more data is input into such a system, it would become increasingly useful for the recognition of synonymies.

It must be stressed that the formula is not a substitute for a formal description or illustration, but it is an aid in the retrieval from a database of all trackways with similar features. Searches could thus be conducted for all trackways with features such as two medial grooves, imprint series of five, or trifold imprints. It has not been the intention to make the formula so complex that a trackway can be accurately drawn from the formula, but a close approximation could be constructed.

DISCUSSION

Proliferation of described ichnogenera of arthropod trackways is increasing present confusion of nomenclature. Many of the forms described in the early days of ichnology, and summarized and illustrated in Häntzschel (1975), are inadequately defined and illustrated in the original publications. Many genera are founded on very small numbers of specimens and intrageneric or intraspecific variation is not defined. If it was made a requirement that only five trackways of reasonable length (say with five set repeats) were needed to erect a new genus or species, the number of new descriptions would fall, but some interesting trackways would probably remain undescribed.

The number of variable features represented in the Description Report Form (Text-fig. 4) and the Trackway Data System can be combined to produce an enormous number of distinctive trackways, which many authors would consider of ichnogeneric or ichnospecific distinction. However, the proliferation of poorly described trackway ichnogenera does not advance our understanding of trackways, nor does it result in the scientific use of the bulk of existing names. The system proposed here is intended to reduce the number of genera and species to more manageable proportions.

Clearly, a drastic revision is required and this is probably outwith the scope (time and travel budget) of any individual. Inevitably revisions will be done in sections by interested individuals with taxonomic, palaeoenvironmental, or stratigraphical interests.

If genera are carefully described and non-restrictive revised diagnoses carefully constructed, the process of revision of trackway ichnogenera can proceed. It is hoped that the use of standard descriptive terms and the Trackway Data System will allow simple keys and computer aided systems for generic and specific identification to be constructed for trackway groups or stratigraphical formations, and ultimately for all arthropod trackways. The main drawback experienced by the author is the inadequate nature of illustration and description of many named forms. The system

TEXT-FIG. 6. Examples of trackways and their description formulae as derived from Text-fig. 5. A, *Octopodichmus didactylus* Gilmore, 1927; Arizona; Permian, Coconino Sandstone. B, *Octopodichmus raymondi* Sadler, 1993; Arizona; Permian, Coconino Sandstone. C, *Paleohelcura tridactyla* Gilmore, 1926 (from Brady 1947); Arizona; Permian, Coconino Sandstone. D, *Siskemia bipedicula* Smith, 1909 (from Walker 1985); Dunure, Scotland; Devonian, Lower Old Red Sandstone. E, *Kouphichnium* sp. Bavaria, Germany; Jurassic, Sölnhofen Limestone (author's collection). F, *Petalichnus capensis* Anderson, 1975; Brandenburg, Cape Province, South Africa; Ordovician, Table Mountain Sandstone (example with internal discontinuous mark - not present in all examples). G, *Palmichnium kosinskiorum* Briggs and Rolfe, 1983; Elk County, Pennsylvania; Carboniferous. H, *Diplichnites gouldi*, Western Australia; Silurian, Tumblagooda Sandstone; Western Australian Museum, No. 84.1634. All scale bars in cm.

advocated will thus require the cooperation of many ichnologists working to a common end by redescribing existing type material, and rejecting genera founded on material inadequate by modern standards.

I would welcome discussion and testing of this proposed system, so that it can be refined, if necessary, and grow into useful user-friendly database for ichnologists.

Acknowledgements. My thanks to all who have ever argued or discussed with me the names of arthropod trackways! Particular thanks to Ian Rolfe and John Pollard for many useful comments and suggestions on the original version. Barry Fulton patiently guided the figures through their evolution, and Karen Chalmers and Susan Simm processed the words.

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